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Year-round haul-out behaviour of male walruses *Odobenus rosmarus* in the Northern Barents Sea

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ABSTRACT: Haul-out behaviour is a central component in the life history of pinnipeds; seasonal patterns in this behaviour reveal insights into annual energy budgets and basic biology. In this study, custom-designed satellite-relay data loggers were deployed on 17 male walruses *Odobenus rosmarus* in Svalbard, Norway. Individual animals transmitted data for a mean ± SD of 255 ± 132 d (range = 54–471 d), performing on average 110 ± 65 haul-out events (range = 30–247 events); the data records for 5 animals were longer than 1 yr. Clear seasonal patterns occurred in the percentage of time hauled out and average haul-out duration; both variables reached maxima in summer and minima in winter. Time between haul-out events reached a maximum during the breeding season in winter. The walruses moved away from shore-based haul-out sites and onto sea ice in November and December, and returned to land again in June. Analyses using generalized additive mixed models and Cox proportional hazard models demonstrated that wind chill and time in the water prior to a haul-out event had the largest impacts on haul-out probability and duration, although wind chill had little impact during the summer when temperatures were not challenging, and also had reduced influence during the breeding period. Long periods at sea were followed by long periods hauled out, resulting in a relatively constant proportion of time spent hauled out over time scales of weeks. Our results indicate the importance of breeding in dictating male haul-out patterns during winter, and provide a baseline to assess impacts of future climate change.

KEY WORDS: Arctic · Biotelemetry · Cox proportional hazard models · Generalized additive mixed models · Marine mammals · Pinnipeds · Svalbard

INTRODUCTION

Pinnipeds (true seals, fur seals, sea lions and walruses) have a unique dichotomy in their life cycles. They spend a significant amount of their time at sea where they forage, but they must come onto a solid substrate (land or ice) for various phases of their life cycle, such as giving birth, nursing (most species), mating (some species) and moulting, and most species spend the majority of their resting time hauled out as well (Bartholomew 1970). Time spent on solid substrates (i.e. hauling out) also facilitates thermoregulatory balance under some environmental conditions, and allows pinnipeds the opportunity to avoid aquatic predators (e.g. Fay & Ray 1968, Riedman 1990).

Haul-out behaviour in most pinniped species has a seasonal pattern; understanding these patterns is vital to: (1) gain knowledge on the timing of important life-cycle events; (2) understand seasonal energy budgets; and (3) document the relative importance of key habitats on an annual cycle for management and conservation planning. Information on the relative proportions of the population hauled out is also useful when calculating correction factors for population abundance assessments; knowledge of how this proportion changes annually is vital for choosing the time of year to perform population surveys, which usually target peak haul-out periods. Birthing, nursing and moulting periods are times of the year when pinnipeds usually haul out most (Riedman 1990). The frequency of haul-out events over the remainder of

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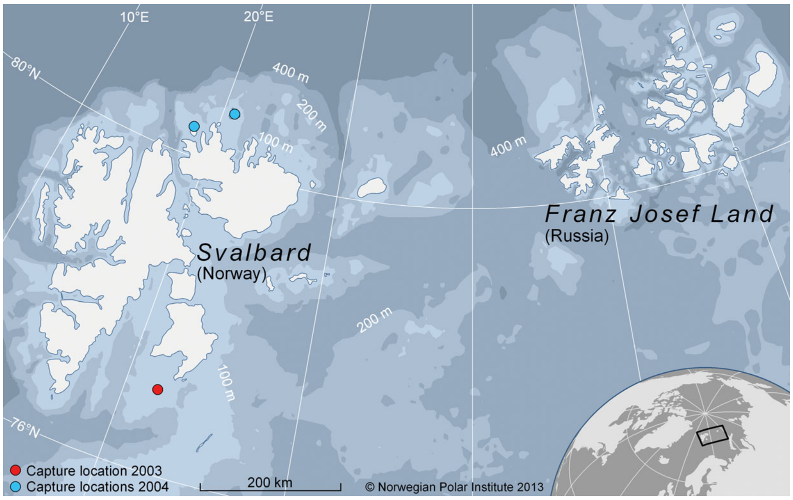

Fig. 1. Svalbard, Norway, and Franz Josef Land, Russia, showing the capture locations for 17 male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in 2003 and 2004

the annual cycle varies greatly among species. Some pinnipeds, such as harp seals *Pagophilus groenlandicus* and Ross seals *Ommatophoca rossi*, undertake long migrations and can remain pelagic, without hauling out to rest, for many months (Ronald & Dougan 1982, Blix & Nordøy 2007). Other pinniped species, such as harbour seals *Phoca vitulina* and Weddell seals *Leptonychotes weddellii*, haul out routinely, almost daily, throughout the year (Andrews-Goff et al. 2010, Hamilton et al. 2014), thus limiting their range to areas close to suitable haul-out platforms. The reasons for the extreme variability in haul-out behaviour among pinniped species is not known, but may be linked to factors such as distribution of their prey, digestion, thermoregulation or predator avoidance.

Walruses *Odobenus rosmarus* are an arctic species with a discontinuous circumpolar distribution; 2 subspecies occupy the North Atlantic and North Pacific regions, respectively. They haul out gregariously on sea ice or at traditional haul-out sites on land regularly throughout the year (Fay 1982). Walruses are predominantly benthic feeders, which generally restricts their range to shallow water areas of less than 100 m depth (Loughrey 1959, Mansfield 1959, Fay 1982). Walruses use sea ice preferentially as a haul-out platform, abandoning it for land only when the sea ice retreats too far from their foraging grounds (Popov 1958, Loughrey 1959, Mansfield 1959, Fay 1982, Jay et al. 2012).

Walrus haul-out behaviour has been shown to be dependent on environmental conditions, with walruses preferring to haul out during periods with low wind and warm temperatures (Mansfield 1959, Salter 1979, Fay 1982, Born & Knutsen 1997, Udevitz et al. 2009). A circadian rhythm has also been detected in some studies, with walruses preferring to haul out during the afternoon and evening (Salter 1979, Born & Knutsen 1997, Udevitz et al. 2009). Walrus haul-out groups are usually 1 of 2 types, either all-male groups or groups that are heavily dominated by adult females with calves and juveniles (Fay 1982).

The walruses in the Svalbard (Norway) and Franz Josef Land (Russia) archipelagos belong to a single population (Fig. 1, Andersen et al. 1998). In Svalbard, walruses occupy traditional terrestrial haul-out grounds when the sea ice retreats away from foraging areas in the summer. They are currently found at a small fraction of the number of haul-out sites that they once occupied, because the population was severely overexploited during a period of hunting that started in the beginning of the 17th century and continued until the walruses were protected in 1952 (Gjertz & Wiig 1994). A recent aerial survey found that about 3900 walruses from this population occur in the Svalbard region during summer (Kovacs et al. 2014). Walruses in Svalbard are predominately males while the majority of females and calves in this population are found in Franz Josef Land. Females were once more numerous in the south-eastern part of the Svalbard Archipelago than they are today (Wiig et al. 2007). Adult male walruses from Svalbard have, not unexpectedly, been shown to migrate towards Franz Josef Land during the winter for breeding (Wiig et al. 1996, Freitas et al. 2009). Summer movements between these 2 archipelagos have also been documented (Wiig et al. 1996, Freitas et al. 2009).

Studies comparing seasonal haul-out behaviour of walruses do not exist at this time. Most studies on walrus haul-out behaviour cover only the summer or early autumn period. Direct observations of walruses are difficult outside these time periods, because of the darkness during the arctic winter and the fact that walruses move away from shore out onto sea ice. Biotelemetry studies on walruses have proven to be challenging, with most data records lasting for periods of less than a few months (Born & Knutsen 1997, Jay et al. 2001, 2006, 2012, Born et al. 2005, Jay & Hills 2005, Udevitz et al. 2009). However, in the present study, year-round haul-out behaviour data of adult male walruses from Svalbard were obtained and analysed to determine (1) how haul-out patterns change over the course of the year and (2) how haul-out probability and haul-out durations are affected by environmental conditions. The latter aspect is particularly important for predicting future climate change impacts.

MATERIALS AND METHODS

Capture and instrumentation

Seventeen male walruses were captured in Svalbard, Norway (Fig. 1), in August 2003 (n = 9) and 2004 (n = 8) and equipped with custom-designed satellite-relay data loggers (SRDLs, Sea Mammal Research Unit, University of St Andrews, St Andrews, Scotland; Table 1). The SRDLs were fitted onto the left tusk of each study animal. For details on capture, chemical immobilization and instrumentation see Lydersen et al. (2008). The SRDLs gave information on the walruses' locations and their dive and haul-out behaviour. Data were received via the ARGOS satellite system (Service Argos, Toulouse, France; see CLS 2011). The tags were programmed to send data whenever possible, with a limit of 250 transmissions d^{-1} in the first 100 d of deployment and not exceeding 140 transmissions d^{-1} thereafter. All animal-handling protocols were approved by the Governor on Svalbard and the Norwegian Animal Research Authority.

Variables used in haul-out behaviour analyses

A haul-out event was defined as any period in which the wet-dry sensor (triggered by a salt water switch) on the SRDL was dry continuously for ≥15 min (sensors were checked every 4 s); this limit was set in order to avoid counting time in the shallows in front of haul-out sites as time on shore. A haul-out event ended when the sensor was continuously submerged in sea water for at least 40 s; this limit was set as it is a reasonable period to assume that the walrus has re-entered the water. The haul-out data transmitted by the SRDL was a start and end time for each haul-out event. Two consecutive haul-out events that had end-to-start times that were less than 15 min apart were combined and treated as a single haul-out event. The SRDLs assign consecutive numbers to haul-out events, which makes it possible to determine whether any haul-out events were not transmitted during a given time period (i.e. a sequence of 10, 11, 12, 13 indicates that all haul-out events in that time period were transmitted while a sequence of 10, 13 indicates that 2 haul-out events, i.e. numbers 11 and 12, were not transmitted) to ARGOS. Missed haul-out events were added to the haul-out record when this was possible, using a com-

Table 1. Summary information from satellite-relay data loggers deployed on 17 male walruses *Odobenus rosmarus* in 2003 and 2004 in Svalbard, Norway. Dates are dd-mm-yyyy

Walrus ID	Start date	Tag life (d)	Tusk volume (cm^3)	Haul-out events transmitted (n)	Haul-out events transmitted (%)	No. of haul-out events added	Total haul-out event coverage (%)
Beck	06-08-2003	271	326	138	92	6	96
Clapton	05-08-2003	193	431	96	90	10	99
Gallagher	06-08-2003	190	552	88	97	3	100
Green	06-08-2003	444	810	193	91	14	98
Hendrix	06-08-2003	179	547	76	97	1	99
Lee	06-08-2003	210	393	94	95	1	96
Vaughan	06-08-2003	232	402	99	93	3	96
Winther	05-08-2003	444	353	247	93	10	97
Zappa	06-08-2003	438	345	169	88	13	95
Mean ± SD		289 ± 118		133 ± 58	93 ± 3	6 ± 6	97 ± 2
Albert	05-08-2004	175	–	73	65	9	73
Bob	05-08-2004	124	412	33	67	2	71
George	04-08-2004	54	–	33	100	0	100
Hubert	05-08-2004	197	514	71	88	5	94
Melvin	05-08-2004	173	433	77	93	4	98
Orval	04-08-2004	402	1146	119	85	9	91
Samuel	04-08-2004	139	479	30	61	4	69
Theodore	05-08-2004	471	456	228	82	18	89
Mean ± SD		217 ± 143		83 ± 66	80 ± 14	6 ± 6	86 ± 12

bination of (1) the data summary table generated by the SRDLs, which records what percentage of time a walrus spends hauled out, diving and swimming at the surface of the water during 6 h intervals; and (2) location data, which informed the selection of the most likely location for missed haul-out events.

The walrus location data were filtered using the speed-distance-angle filter from Freitas et al. (2008) in the R 3.0.1 (R Core Team 2013) argosfilter package using the default settings (Freitas 2012). Additionally, locations that were suggested to be >5 km inland were assumed to be erroneous and were removed using ArcMap10 (ESRI); most such locations were actually >10 km from the shoreline. If there were location(s) transmitted during the course of a haul-out event, the location with the highest ARGOS location quality was chosen to represent the haul-out location. If multiple high-quality locations were transmitted during a single haul-out event, the haul-out location was calculated as the average of these locations. If there were no location fixes transmitted during a haul-out event, the haul-out location was calculated via linear interpolation along the track line based on time. Implausible haul-out locations (i.e. locations in the open sea during periods when sea ice was not believed to be present) were moved to the most likely land mass given the walrus' track.

Potential explanatory variables used in the analyses of haul-out behaviour are listed in Table 2. Air temperature, wind speed and air pressure were extracted from the Norwegian Meteorological Institute's atmospheric and wave archive for Norwegian and surrounding areas (NORA10). The temporal resolution of this archive is hourly, and the spatial resolution is ~11 km (Reistad et al. 2011, Haakenstad et al. 2012). Weather data were extracted for the temporal midpoint of each walrus haul-out event and inter haul-out period if these periods were less than 24 h, and 1 additional weather data point was added for every additional 12 h of haul-out/inter haul-out period. If there was more than 1 temporal point selected for the haul-out or inter haul-out period, these points were evenly spaced within the time period. The locations for the inter haul-out points were calculated via linear interpolation along the track line based on time.

Daily sea ice shape-files from the Norwegian Meteorological Institute (NMI; http://polarview.met.no/) were imported into R. NMI separates the sea ice concentration into 6 categories: (1) 0–9%; (2) 10–39%; (3) 40–69%; (4) 70–89%; (5) 90–99%; and (6) 100%. Individual walrus haul-out locations were categorised based on their locations into 1 of 3 substrate categories: (1) land; (2) ice concentration below 40%; and (3) ice concentration above 40%. The 40% ice cover separation was set in an attempt to separate haul-out events that were almost certainly on sea ice from those that may have either been on sea ice near shore or on shore. Early and late in the sea ice season, when walruses are making the transition between sea ice and land as a haul-out substrate, the accuracy of the sea ice shapefiles and the ARGOS locations makes it difficult to determine the haul-out substrate with certainty.

Tusk volume was included in the study as a rough proxy of age (Fay 1982). Tusk length and circumference at the base were measured to the nearest cm and, assuming that walrus tusks are cone-shaped, the following equation was used to calculate tusk volume (V):

Table 2. Continuous variables, including their abbreviations, units, resolutions and sources, used in the analyses of haul-out behaviour of 17 male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in Svalbard, Norway, in 2003 and 2004; M&M: 'Materials and methods: Variables used in haul-out behaviour analysis' section in the main text

Variable	Abbreviation	Units	Resolution	Source
Air temperature	temp	°C	See M&M	Norwegian Meteorological Institute (www.met.no)
Wind speed	wind speed	$m\ s^{-1}$	See M&M	Norwegian Meteorological Institute
Air pressure	pressure	hPa	See M&M	Norwegian Meteorological Institute
Wind chill[a]	wind chill	°C	See M&M	Temperature and wind speed data
Solar hour	shour	h	h	local2Solar function in solaR library in R.2.15.2
Month	month		mo	This study
Tusk volume	tvol	cm^3	cm	Freitas et al. (2009)
Aquatic time before a haul-out event	lasth	Atomic time	min	This study
Duration of previous haul-out event	lastdur	Atomic time	min	This study

[a] $T_{wc} = 13.112 + 0.6215 \times T_a - 11.37 \times V^{0.16} + 0.3965 \times T_a \times V^{0.16}$ (T_{wc} = wind chill, T_a = ambient temperature [°C] and V = wind speed [km h^{-1}]; Environment Canada, http://climate.weather.gc.ca)

$$V = \frac{1}{3}\pi r^2 h \quad (1)$$

where r and h represent the radius and length of the tusk, respectively.

Correlation coefficients and variance inflation factors (VIFs) were calculated for all covariates, with VIFs above 3 considered to be high values (Zuur et al. 2009). Pairs of covariates that were highly correlated were not both included in the same model. Data exploration was carried out as recommended by Zuur et al. (2010). Data were analysed using R 3.0.1 (R Core Team 2013), and all results are presented as mean ± 95% confidence intervals (CI), except where stated otherwise. All maps were made using ArcMap10 (ESRI). The 5 walruses that transmitted data for over 1 yr occur twice in the months that had data in consecutive years.

Monthly haul-out indices

Mean and 95% CIs were calculated for different monthly haul-out indices: (1) percentage of time hauled out; (2) haul-out duration; (3) time between haul-out events; and (4) proportion of haul-out events on various substrates. The CIs were bootstrapped (1000 repetitions) using the boot package (Canty & Ripley 2012) in R because the data were not normally distributed. Bootstrapped means were calculated twice, firstly for individuals and secondly for all walruses to account for the repeated measures nature of the data. The plots produced by the jack.after.boot function in the boot package were used to assess the influence that each walrus had on the bootstrap results.

Haul-out probability

To analyse the probability of hauling out relative to environmental, temporal and physiological covariates, the data record for each walrus was divided into 1 h intervals, and a walrus was considered hauled out for a given hourly bin if it was hauled out for the majority of the time. Data exploration revealed nonlinear relationships between haul-out probability and solar hour. In order to accurately characterize this relationship and the annual patterns in it, a generalized additive mixed models (GAMM; Wood 2006) were used.

The GAMMs were modelled using the mgcv package in R. The response variable was included in the model with a logistic link, and the binomial family was used to assess the residual variance (Wood 2006). Wind chill, air pressure, tusk volume and solar hour were included as fixed effects. Solar hour was added using a cyclic cubic regression spline to ensure circularity of the variable; a k (k is the basis dimension of the smooth term which sets the upper limit (k−1) of the degrees of freedom associated with a smooth) of 4 was chosen to ensure that the relationship could be accurately characterized. Walrus ID and year were included in the models as nested random effects. An autoregressive model of order 1 (corAR1) structure was used to model the temporal autocorrelation, with walrus ID included as a grouping factor (Zuur et al. 2009). The same model was run for each month to examine the effect of the covariates on haul-out probability over the course of the year. Tusk volume and solar hour did not significantly impact haul-out probability in any month, so these variables were not included in the monthly-run models. In January, k was increased to 5 and in October, solar hour was modelled as a cubic regression spline term with a k of 4 to achieve model convergence.

All models were investigated for goodness of fit. Because residuals from binary models are difficult to interpret, the fitted values, raw data, deviance and normalized residuals were grouped by walrus ID and day to verify model fit (Zuur et al. 2009). The normalized and deviance residuals were plotted against each variable included and excluded from the model. To verify that the k value in the smooth term was high enough, the smooth term was applied to the deviance residuals with an increased k to ensure that no pattern remained (Wood 2012). A quantile-quantile plot was constructed to investigate linearity of the random effect.

Haul-out duration

The Cox proportional hazards mixed effects regression model (Cox 1972) was used to assess the relationship between haul-out duration and the covariates mentioned above using the coxme package in R (Therneau 2012; also see the Supplement at www.int-res.com/articles/suppl/m519p251_supp.pdf).

One model was run for each month to assess the varying impact of the covariates on haul-out duration throughout the study period. The covariates included wind chill, pressure, aquatic time before a haul-out event and duration of the previous haul-out event. Walrus ID and year were included as nested random effects (Therneau & Grambsch 2000). To verify goodness of fit, the models for each month were rerun using the survival package in R (Therneau 2013) with the random effects included as shared gamma frailty terms, because residuals are not yet implemented in coxme. The cox.zph function (Therneau & Grambsch 2000) was used to measure the correlation of the scaled Schoenfeld residuals with a time transformation to test the validity of the proportional hazards assumption. Both the p-values and the plots produced by the cox.zph function were investigated. The presence of influential observations was checked using dfbeta residuals, and martingale residuals were used to check for non-linearity of covariates. The martingale residuals were plotted against covariates and used to create partial residual, or component-plus-residual, plots. A local linear regression using a loess smoothing function was used to aid in the interpretation of the martingale residual plots (Therneau & Grambsch 2000, Fox & Weisberg 2011).

RESULTS

Tag life

The mean ± SD period of data transmission from each walrus was 255 ± 132 d (range = 54–471 d; Table 1), during which the animals performed an average of 110 ± 65 haul-out events (range = 30–247 events; Fig. 2, Table 1). On average, 87 ± 12% of the haul-out events were relayed directly via the ARGOS system. Including missing haul-out events that could be well characterized (see 'Materials and methods: Variables used') brought the total average haul-out coverage up to 92 ± 10% (Table 1).

Monthly haul-out indices

The percentage of time hauled out and the average haul-out duration reached maxima in the summer and minima in the winter and early spring (see Figs. 3 & 4). The average time between haul-out events had 2 peaks, a major one in late winter/early spring (Fig. 5), and a secondary, more moderate peak in late summer/early autumn (Fig. 5). Individual variation in time hauled out, haul-out duration and time between haul-out events were generally low, as expressed by only minor variation in the plots produced by the jack.after.boot function.

The walruses used land as their primary haul-out substrate during the summer months, but began to use ice when it appeared around haul-out sites in November and December. They continued to haul out on sea ice throughout the winter and spring, until they returned to shore in June when sea ice retreated northward off the shelf and into the deep Polar Basin, where conditions are unsuitable for walrus feeding (Figs. 2 & 6). Again, the individual variability in these choices was quite low, except during months where substrate transition was taking place.

Haul-out probability

Wind chill had the largest effect of any of the environmental variables on haul-out probability, with higher values leading to decreased haul-out probabilities for all months from September to June (Table S1 in the Supplement at www.int-res.com/articles/suppl/m519p251_supp.pdf). Walruses had an increased probability of hauling out with increasing air pressure in most months of the year (Table S1). Solar hour had a significant impact on haul-out probability in the late winter and spring (February to May; Fig. 7, Table S1).

Haul-out duration

The duration of time spent in the water prior to a haul-out event significantly affected haul-out duration with a long time at sea generally being followed by a long haul-out duration (Table S2 in the Supplement) during most months of the year. The duration of the previous haul-out event negatively impacted the duration of the next haul-out event in some months (Table S2).

Wind chill did not impact haul-out duration during the summer, but for the rest of the year (except February to April), less wind chill led to longer haul-out durations (Table S2). An increase in air pressure led to longer haul-out durations in some months (Table S2), while no such relationship was found for the rest of the year.

Variability among individuals and years with regards to risk of ending a haul-out event was generally low. Variation in both random effects was greatest in January and February (Table S2).

DISCUSSION

This is the first study to report year-round haul-out behaviour of walruses. Seasonality was detected in this behaviour with regards to percentage of time hauled out, average duration of haul-out events and

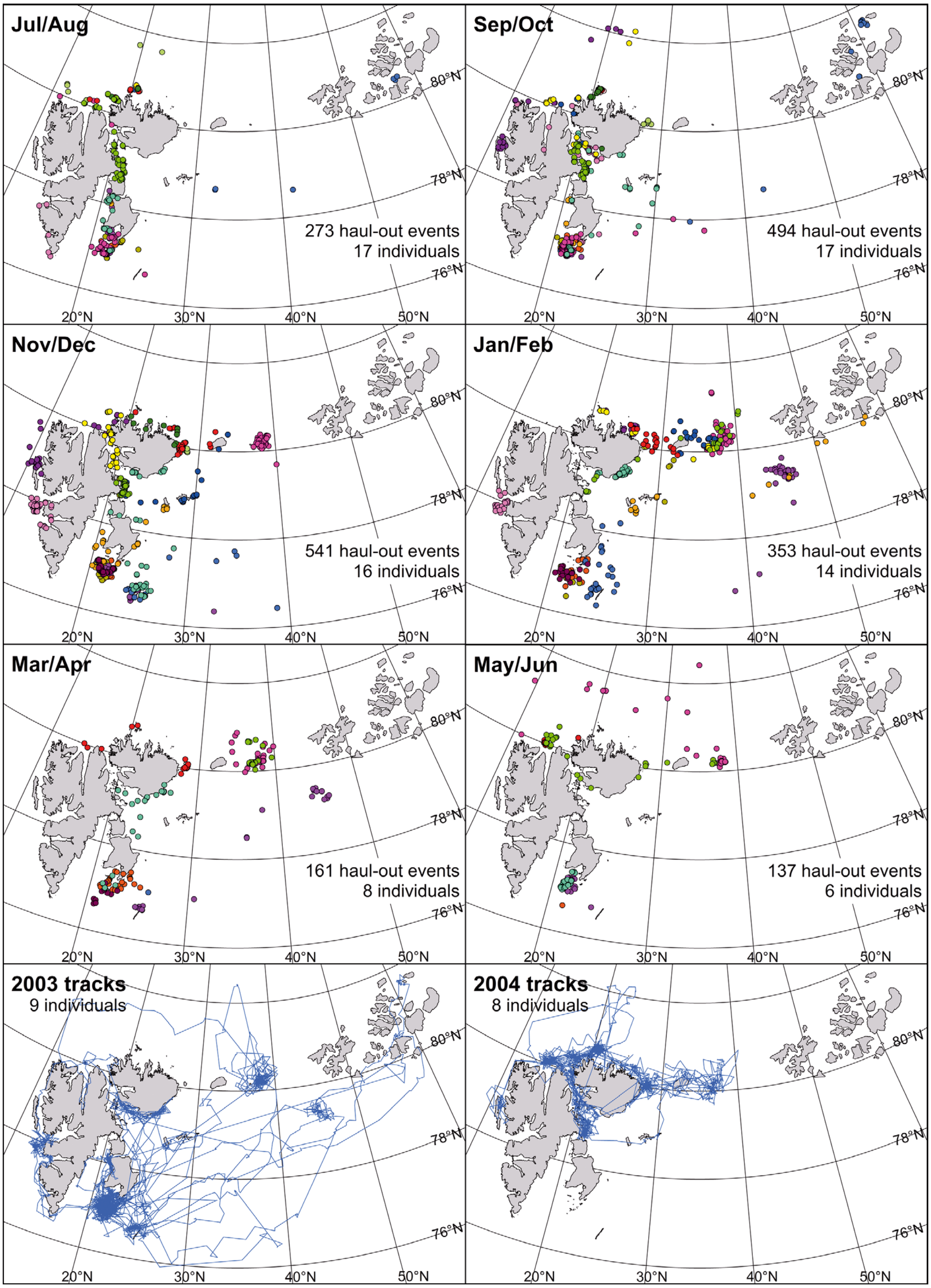

Fig. 2. Haul-out locations for male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in Svalbard, Norway, in 2003 and 2004 by 2 mo intervals. Nos. of haul-out events and individuals are also included. Each individual is portrayed in a unique colour. The bottom 2 plots depict the tracks for each tagging year

average time between haul-out events. There was also seasonality in the substrate used for hauling out; walruses generally left shore-based haul-out sites and used sea ice as a haul-out platform in November and December when sea ice formed around haul-out grounds. They returned to shore again in June when sea ice retreated over the shelf into deep waters north of Svalbard (i.e. into areas unsuitable for wal-

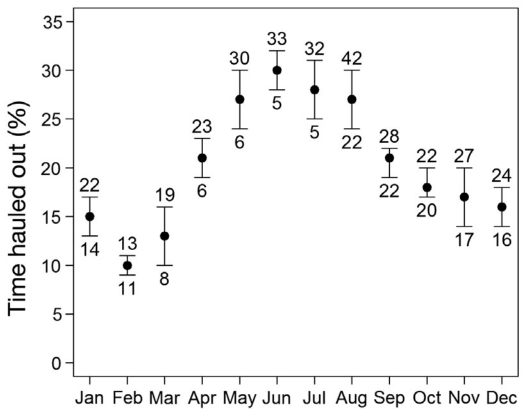

Fig. 3. Percentage of time hauled out (mean ± 95% CI) per month for 17 male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in Svalbard, Norway, in 2003 and 2004. The number at the top of the CI bar indicates the maximum percentage of time an individual walrus spent hauled out in that month, restricted to the walruses that transmitted data for at least 25 d during that month, and the number at the bottom of the CI bar indicates the number of walruses that transmitted data in that month; the 5 walruses which transmitted data for >1 yr were counted twice for the overlapping months in their data records

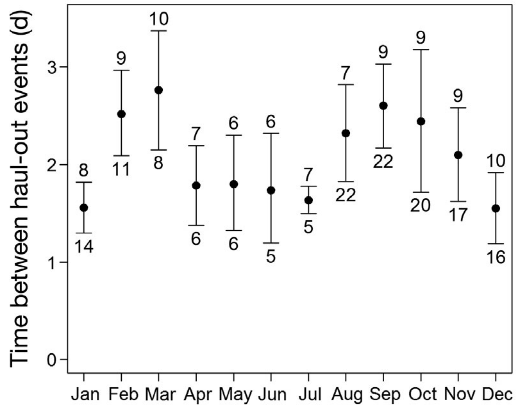

Fig. 5. Average time between haul-out events (days; mean ± 95% CI) for each month for 17 male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in Svalbard, Norway, in 2003 and 2004. The number at the top of the CI bar indicates the maximum inter haul-out period each month. See Fig. 3 for further details

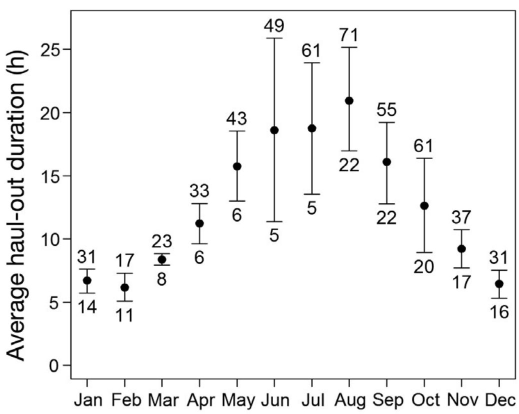

Fig. 4. Average haul-out duration (h; mean ± 95% CI) for each month for 17 male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in Svalbard, Norway, in 2003 and 2004. The number at the top of the CI bar indicates the maximum haul-out duration each month. See Fig. 3 for further details

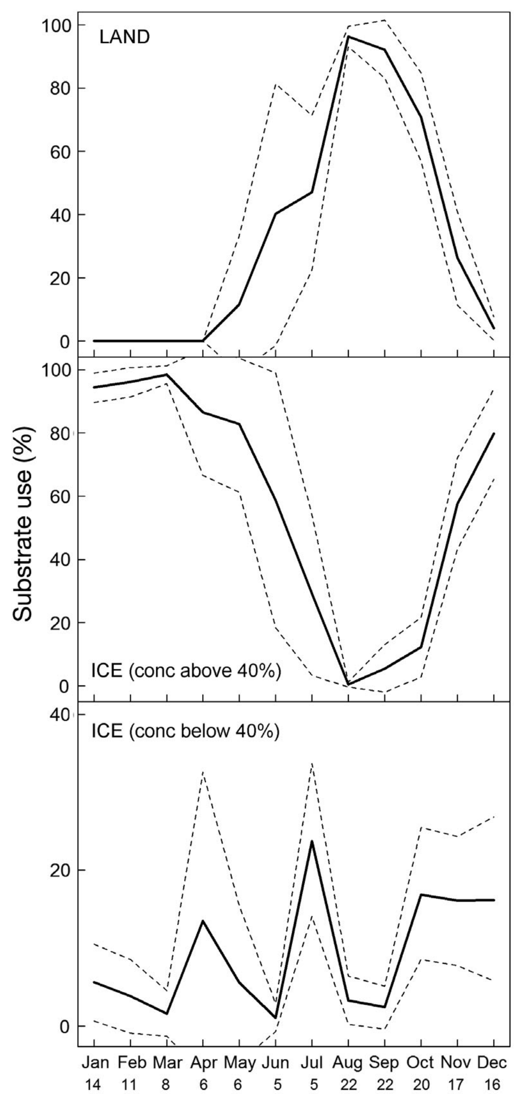

Fig. 6. Proportion of haul-out events (mean ± 95% CI) for each substrate category by month, for 17 male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in Svalbard, Norway, in 2003 and 2004. The numbers below the month labels indicate the number of walruses transmitting haul-out data; the 5 walruses which transmitted data for >1 yr were counted twice for the overlapping months in their data records

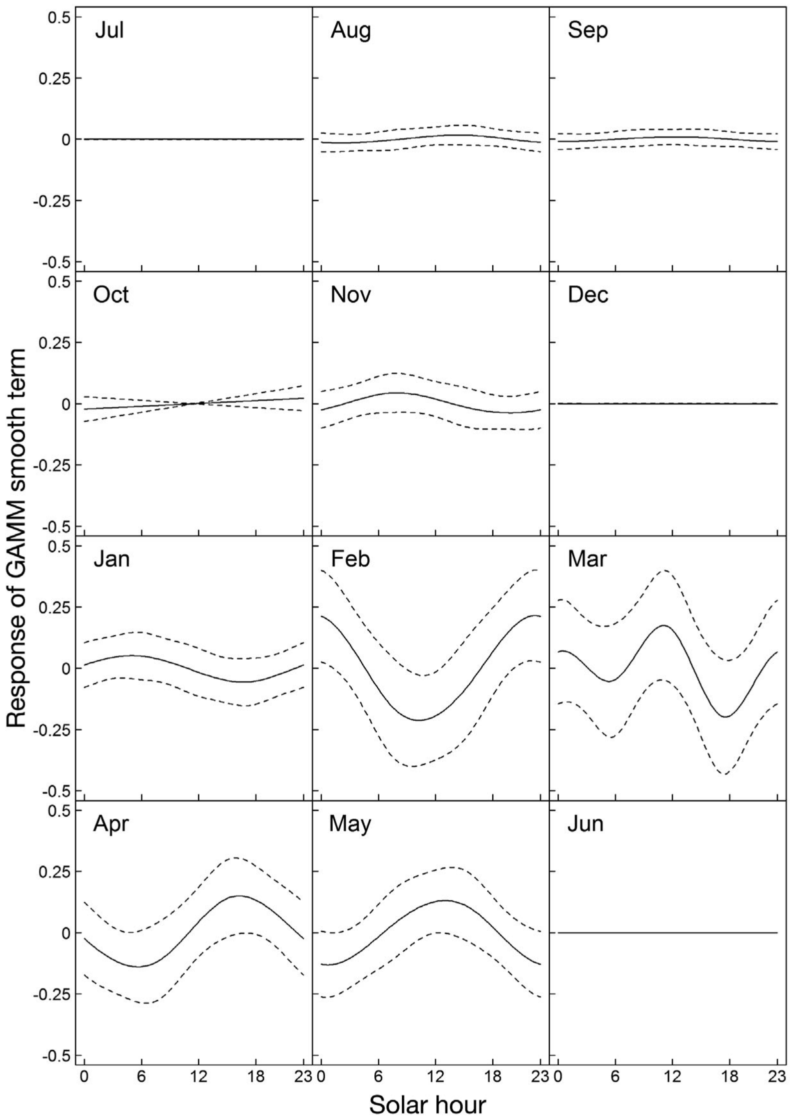

Fig. 7. Response of the generalized additive mixed effects model (GAMM) smooth curve (mean ± 95% CI) to solar hour by month for 17 male walruses *Odobenus rosmarus* equipped with satellite-relay data loggers in Svalbard, Norway, in 2003 and 2004

rus feeding). Documenting haul-out behaviour accurately and well is important for planning of abundance surveys and the creation of correction factors to account for animals in the water at the time of surveys (see Lydersen et al. 2008, 2012, Kovacs et al. 2014).

In the present study, haul-out data coverage from the SRDL records was 92 ± 10%. Observations around terrestrial haul-out sites suggest that it is common for walruses to spend considerable periods of time wallowing in the shallow water in front of haul-out beaches before moving up onto shore (K. Kovacs & C. Lydersen pers. obs.). During these periods, the wet/dry sensor may be dry long enough for registration of a haul-out event, even though the animal technically is not onshore. This would overestimate the time the animals are hauled out, and is a problem that applies to all studies with electronic tags using wet/dry sensors to determine haul-out events. Additionally, walruses are able to inflate their pharyngeal pouches and float/sleep/rest vertically in the water, 'bottling' at the surface; such a posture might also result in the wet/dry sensor reporting a haul-out event when the animal is actually at sea during calm weather. However, both of these behaviour patterns are not likely to inflate haul-out time by any great extent. Approximately 75% of the locations calculated by ARGOS for this study were location quality A and B, which do not have an accuracy estimate. This is common in studies of marine mammals, and research comparing these classes to GPS-based estimates on various pinniped species have found location errors of 6 and 10 km for classes A and B, respectively, although the exact numbers are species specific (Costa et al. 2010). This ARGOS error combined with the weather data being predicted at a ~11 km spatial resolution means that the spatial resolution of the analyses in this study is coarse.

Since this is the only published information based on longitudinal data over entire annual cycles, comparisons of annual cyclicity cannot be made with other areas. However, the average percentage of time hauled out in different months was similar to that found in other temporally discontinuous studies (both sexes: Salter 1979, Udevitz et al. 2009; males: Born & Knutsen 1997, Gjertz et al. 2001, Jay et al. 2001, Born et al. 2005).

The average haul-out durations reported herein for August and September in Svalbard, when the majority of haul-out events are terrestrial, is shorter than those reported from other populations that also haul out on land during these months (16–21 h vs 37–38 h; Born & Knutsen 1997, Jay et al. 2001, for male walruses in Greenland and Alaska, respectively). These durations are similar to the average haul-out durations of walruses hauling out on sea ice in Greenland in August and September (11 h; Born & Knutsen

1997). The walruses tagged by Born & Knutsen (1997) travelled up to 50 km from their terrestrial haul-out sites to forage, but had sea ice in the foraging area during 1 of the 2 years in which this study occurred, which they used for resting before returning to land. Consequently, the walruses were absent from the terrestrial haul-out site longer in the year when sea ice was available than when it was not. Gjertz et al. (2001) determined that male walruses in Svalbard usually foraged less than 2 km from their haul-out sites. The proximity of some of the terrestrial haul-out sites to benthic food sources in Svalbard may explain why the average haul-out duration in the summer months is more similar to walruses hauling out on sea ice near their foraging grounds elsewhere. The average haul-out duration for our male walruses in Svalbard during April was similar to that reported by Udevitz et al. (2009) in the Bering Sea for both male and female walruses; both populations haul out on sea ice during this time of year (Udevitz et al. 2009, this study).

There were seasonal trends in the average haul-out duration and the percentage of time spent hauled out by the walruses in Svalbard; both reached minima during the winter. The average time between haul-out events reached a maximum in February and March. Breeding in walruses occurs sometime between January and April (Fay 1982, Sjare & Stirling 1996, Born 2003), and in Svalbard, breeding areas are located hundreds of km into the pack ice at polynyas, and possibly also at a few sites near the coast of Svalbard (Freitas et al. 2009, A. D. Lowther et al. unpubl. data). The mating system in walruses has been described as female-defence polygyny, in which groups of females and calves are attended by 1 or a few males that perform complex, stereotyped underwater vocalizations (Fay 1982, Sjare & Stirling 1996, Nowicki et al. 1997). Diving bouts with such underwater vocalizations have been recorded to last up to 48 h (Nowicki et al. 1997). The diving behaviour of the walruses in this study exhibited a sudden shift to a larger proportion of shallow dives in the winter compared to the summer period, a diving pattern consistent with breeding behaviour (A. D. Lowther et al. unpubl. data). Their haul-out activity is most likely constrained by their need to perform underwater displays during this period, resulting in a decreased amount of time hauled out and increasing the time between haul-out events compared to other times of the year.

Walruses in Svalbard haul out predominately on land during the summer. However, drift ice is readily used during the summer if it occurs near shore, as it did in the summer of 2005 (Lydersen et al. 2008). Generally, the sea ice retreats north of Spitsbergen in the summer, retracting in recent years to the point where the edge is over very deep waters which are unsuitable for walrus feeding. Three walruses tagged in 2004 travelled to the northern ice during August and September, but only stayed there for a few days before returning to the coastline. A few haul-out events took place during these excursions, which were on ice in waters over 1000 m deep. Other studies also suggest that walruses will abandon their terrestrial haul-out grounds whenever sea ice becomes available (Popov 1958, Loughrey 1959, Mansfield 1959, Mansfield & St. Aubin 1991), although others have found that both substrates are utilized when they are simultaneously available near foraging grounds (Salter 1979, Born & Knutsen 1997). Separating haul-outs by ice concentration at the seemingly arbitrary value of 40% to attempt to minimize the impact of misidentification of haul-out substrate in light ice conditions near shore was not problematic, as the number of haul-out events on ice less than 40% were few, and fluctuated only at very low levels throughout the year.

The dominant factors affecting haul-out behaviour of walruses in Svalbard were wind chill and time spent in the water before a haul-out event. Wind chill, which was used in these models to assess the combined effect of temperature and wind speed, was the dominant environmental variable impacting walrus haul-out behaviour for most months of the year. The only time periods in which it did not have a major influence were during the warmest months of the year (i.e. summer) and during the breeding period in the winter. Other studies do report reduced haul-out in very cold conditions or at high wind speeds for both male and female walruses during the summer (Salter 1979, Born & Knutsen 1997), but the absence of severe storms during the 3 summers in our study area may have limited our ability to detect a similar relationship for walruses in Svalbard. The lack of a dominant effect of wind chill on haul-out behaviour from February to April may be due to the breeding behaviour of the walruses, as factors other than environmental conditions likely drive haul-out behaviour during this time period.

Air pressure significantly affected haul-out behaviour in many months, with a higher air pressure leading to an increased probability of hauling out and a decreased risk of ending a haul-out event. This is not surprising, since high air pressure systems are often associated with calm, fair weather.

A diel patterning of activity has been reported in some walrus populations (both sexes: Fay & Ray 1968, Udevitz et al. 2009; males: Born & Knutsen 1997), but not in all earlier studies (both sexes: Salter 1979; males: Jay et al. 2001). The walrus population in Svalbard occurs farther north than most other studied populations; consequently a 24 h light/dark cycle is only present in the spring and autumn with continual absence or presence of the sun characterizing the winter and summer periods, respectively. In the present study, solar hour affected the haul-out probability of walruses only during late winter and spring. In February, the highest probability of hauling out occurred around midnight, and in March, the highest probabilities occurred around noon and midnight. These patterns are difficult to explain, but may be related to moon light in the winter or perhaps attendance patterns during the breeding period and the return of the sun in March. In the spring (April and May) the walruses preferred to haul out in the afternoon when temperatures are warmest. Temperatures are more benign in autumn than in the spring; the harsher conditions in the spring may have increased the importance of basking in the sun during midday.

The duration of time in the water before a haul-out event positively impacted the duration of the subsequent haul-out in the majority of months. This means that walruses spend a relatively constant fraction of time hauled out over time scales of weeks, as longer time periods spent in the water are followed by longer time periods at rest (i.e. hauled out).

Breeding activity appears to be an important factor driving male walrus haul-out patterns during winter. The male walruses in this study hauled out less and had shorter haul-out events and longer periods in the water between sequential haul-out events during winter. Although this pattern may be due solely to environmental conditions, with walruses escaping extreme weather conditions by getting out of the air and into the more stable marine environment, their response to wind chill suggests that this is not the case. One would expect that wind chill would have its most pronounced impacts during the winter months when conditions are the most severe. However, this was not found to be the case; wind chill had no impact on haul-out duration in these months. About 25 and 50 %, respectively, of haul-out events during this period had temperature and wind chill values colder than −20°C. The lower critical temperature in walruses has been suggested to be about −20°C in light wind conditions (Fay & Ray 1968, Ray & Fay 1968). Thus, male walruses might experience extra thermoregulatory costs during the limited time periods that they do haul out in these months, increasing the amount of energy expended during this important period. Breeding is an energetically demanding time period for the males of most pinniped species; males expend large amounts of energy in order to defend territories or monopolize groups of females (Riedman 1990).

All marine mammals endemic to the Arctic are associated with sea ice for various aspects of their life cycles. Thus, the current and expected future declines in sea ice extent are a serious concern with regards to future abundance and distribution of these animals (Kovacs et al. 2011). Sea ice declines have resulted in increased use of terrestrial haul-out grounds for walruses in the Bering and Chukchi Seas (Jay et al. 2012, MacCracken 2012). This has likely occurred in other Arctic areas as well, without detection because of a lack of monitoring. Most walruses in Svalbard use terrestrial haul-out grounds in the summer, but a decrease in the duration of the sea ice season will increase the time period in which walruses occupy these sites and adjacent feeding areas. This situation will be magnified with continued sea ice declines, potentially resulting in walruses decreasing their prey bases near terrestrial haul-out areas and also potentially facing increased impacts of mortality caused by stampedes at haul-out sites (MacCracken 2012). An additional issue for walruses in Svalbard concerns the breeding migration towards Franz Josef Land. Delays in the formation of suitable ice might result in a mismatch between the availability of ice and the physiological timing of breeding.

Future warming in the Arctic might also decrease the amount of pelagic–benthic coupling and shift systems from sea-ice algae–benthos-dominated systems to phytoplankton–zooplankton-dominated systems, resulting in decreased benthic biomass (Piepenburg 2005). This would reduce environmental carrying capacity for species such as walruses which feed on the benthos, potentially resulting in decreased abundance or a larger proportion of the population exploiting alternative food sources such as seals and seabirds (Lowry & Fay 1984, Gjertz 1990).

In this study, we found strong seasonal patterns in male walrus haul-out behaviour with regards to percentage of time hauled out, haul-out duration and time between haul-out events. Walruses in Svalbard use sea ice as a haul-out substrate throughout most of the year, but haul out on land in the summer when the sea ice retreats away from their shallow-water, coastal foraging areas. Time in the water before a haul-out event had a significant impact on haul-out duration, with longer periods at sea being followed by longer periods hauled out. Wind chill also affected haul-out behaviour throughout much of the year, but had a reduced impact during the summer when weather conditions are mild and also during the mating period when male behaviour seems to be dictated by their aquatic breeding strategy. Data from female walruses would reveal further insights into seasonal haul-out patterns and constraints on females with young of various ages, and also highlight differences between the 2 sexes because of body size or other factors. Year-round data on walrus haul-out behaviour from other regions would facilitate geographic comparison, and also provide a basis for detecting changes in relation to reductions in Arctic sea ice extent across the species' range.

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